The Mushroom Body Pathway within a Chemotaxis Sensory-motor Loop

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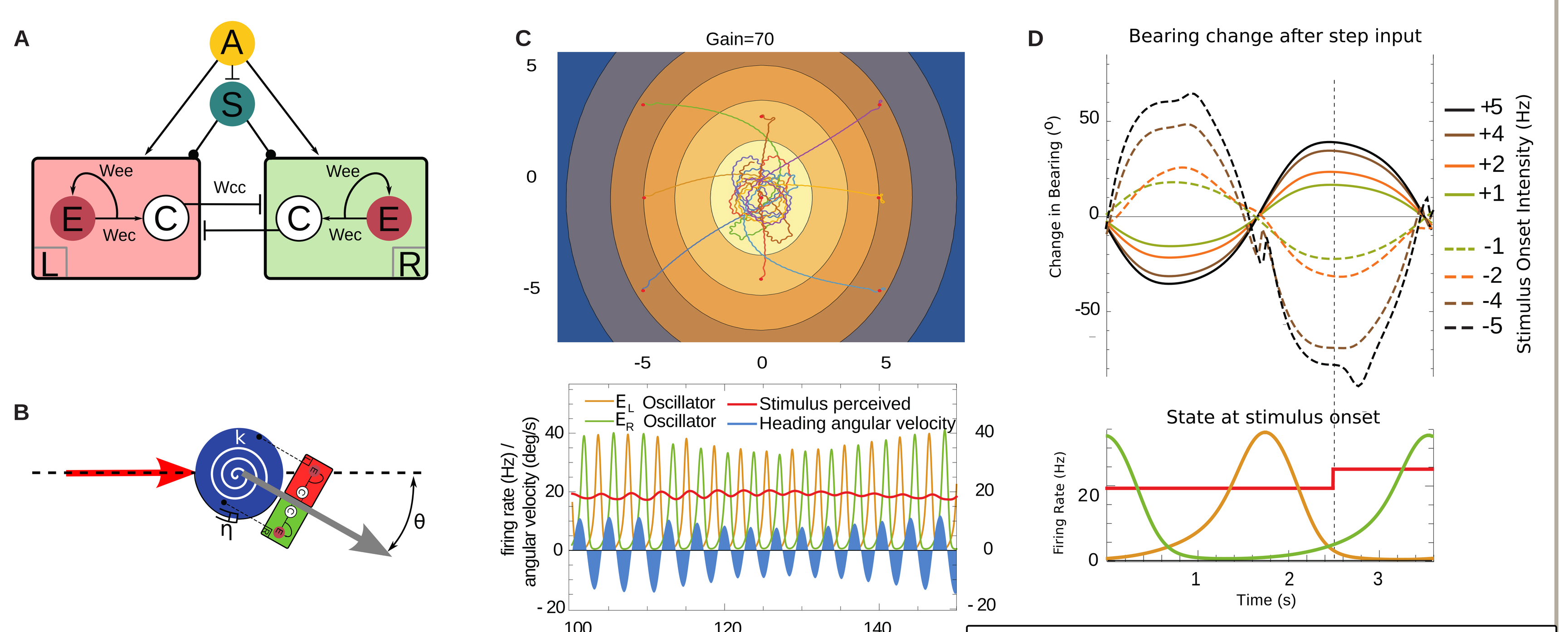
Background

A Neural oscillator based sensory-motor loop



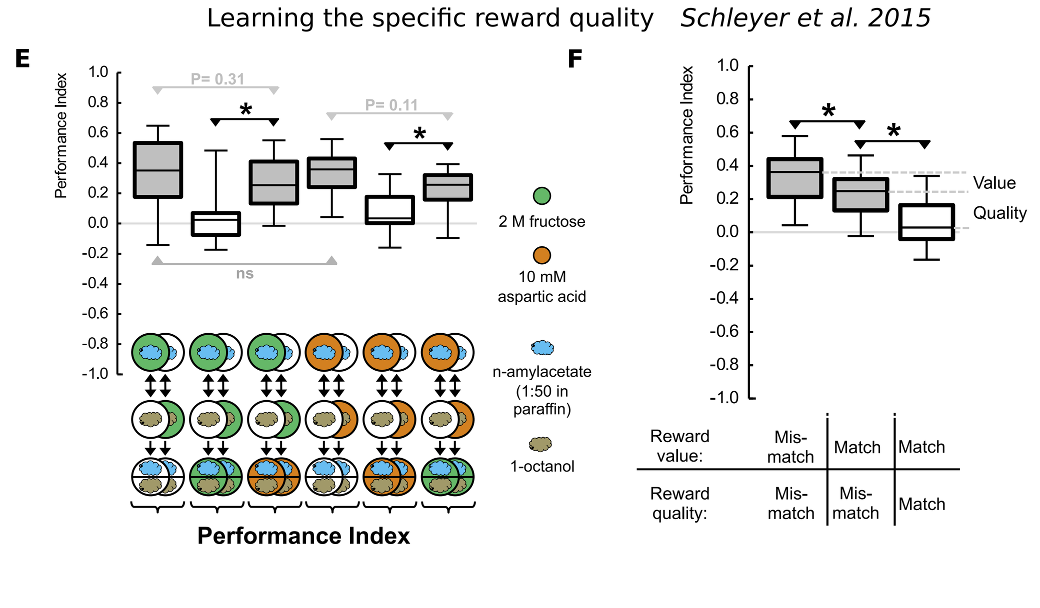
A sensory-motor loop consisting of a neural oscillator (A) that is perturbed by converging sensory signals is sufficient to produce taxis in stimuli gradients (C).

(D) uses step stimuli to show that the change of bearing depends on stimulus timing.

Learning
Larva's odour preference can be modified via associative learning. Training achieved by pairing odour to a gustatory reinforcer.

Memory Recall & Suppression
Appetitive learning induced changes in odour preference are suppressed in the presence of the reinforcer quantity and quality matching the one used during training (E,F) (Schleyer et al. 2015).

Learning the specific reward quality *Schleyer et al. 2015*

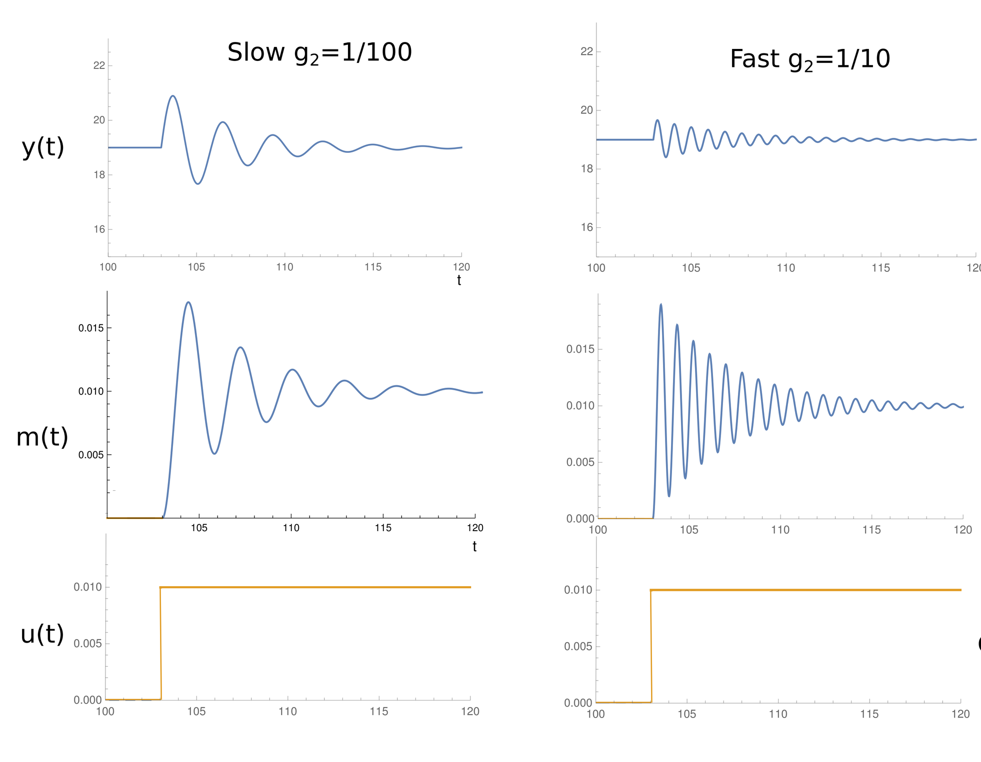


Research Question

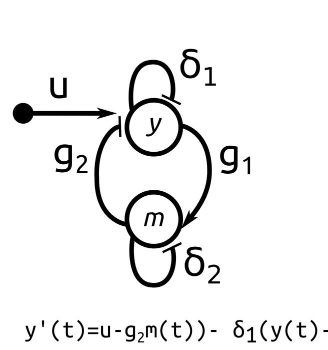
The neural oscillator relies on stimulus timing to drive effective steering.
How does the memory engram modify the sensori-motor loop to change odour preferences?

Circuit has only been tested by directly coupling to the input stimulus.
However, neural output commonly has delay and feedback dynamics.
Would these compromise the ability of the oscillator to steer when driven by neural circuits?

Methods



We introduce feedback dynamics to replace the artificial direct input-feed to the oscillator.
These act to adapt output to operate around a set-point.
We check if the stimulus-timing is compromised, and if chemotaxis works.

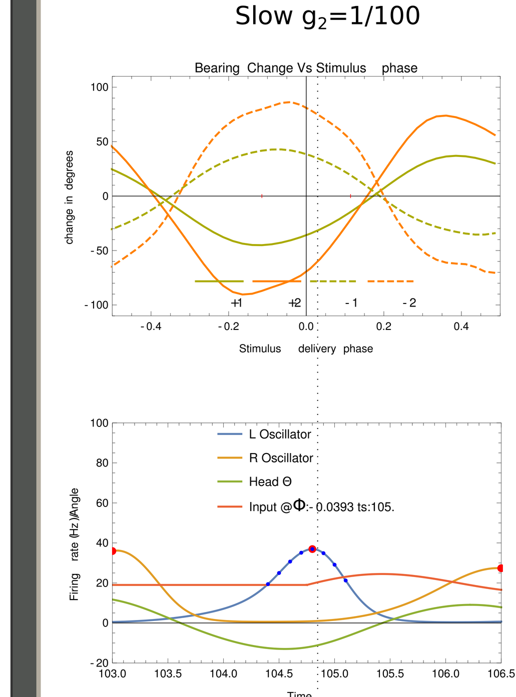


$$y'(t) = u - g_2 m(t)) - \delta_1(y(t) - b)$$
$$m'(t) = g_1(y(t) - b) - \delta_2\, m(t)$$

Common integrative feedback model that generates output adaptation around set point b. Let $g_2 < 1$, $g_1 = 1$

Effects of input dynamics

Slow g_2=1/100



Using a fully adapting integral feedback to processes the input allows changes in stimulus to be detected as the agent moves in the gradient.

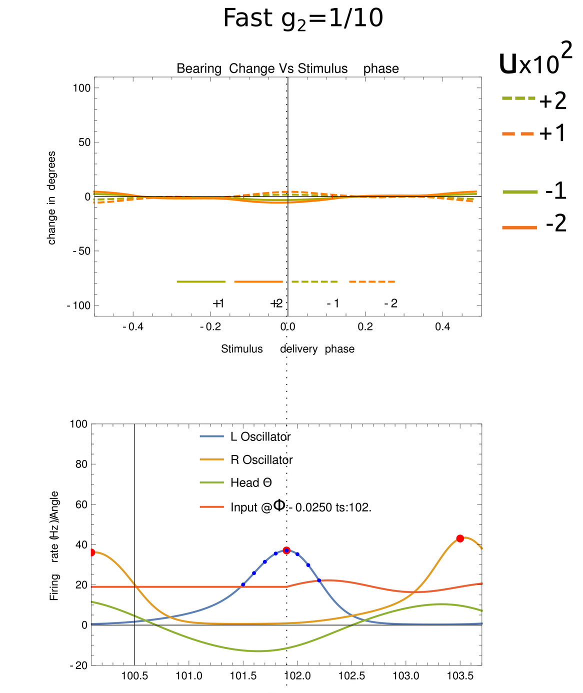
Pertubating input around a set point is exactly what the oscillator requires, and thus such feedback could be employed to maintain the set point.

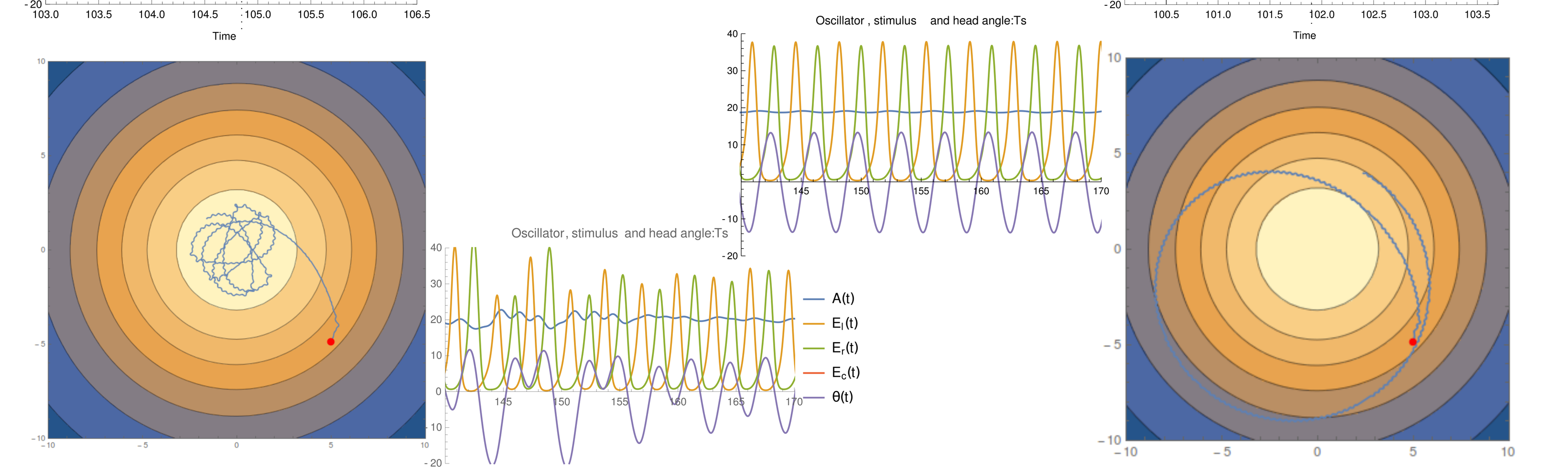
We found this to be sufficient for chemotaxis, yet it appears performance depends on the dynamics of the input not just its magnitude.

Increasing the feedback gain g_2 or g_1 makes reduces chemotaxis and steering ability, while the system response becomes faster.

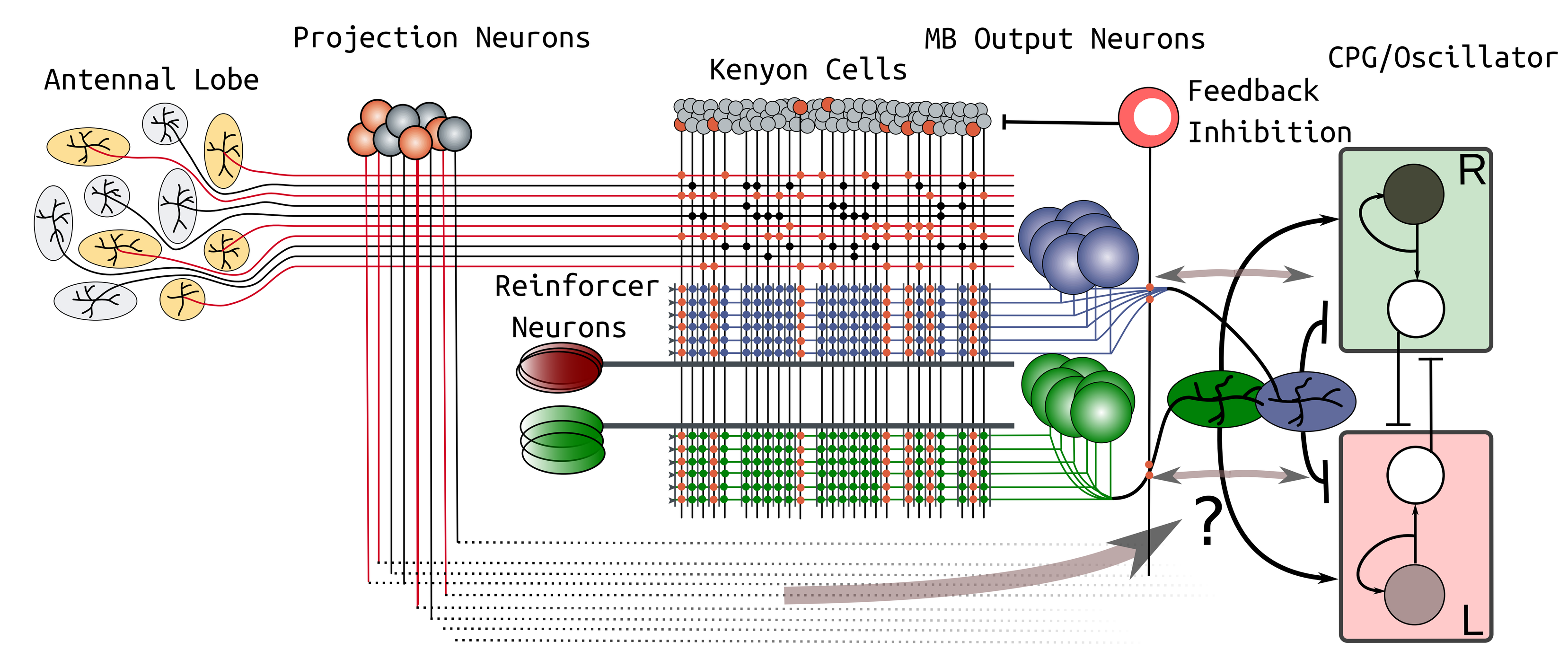
This system could be implemented in circuits with populations of inhibitory and excitatory neurons.

Fast g_2=1/10





MB Hypothesis



Adapted from Heseinberg et al. 2013

MB circuit maintains the oscillator's input set point.
Synaptic plasticity can be seen as changing the feedback loop gains, in an odour specific manner.
MBONs valence is differentiated on whether it reaches the oscillator via an excitatory/inhibitory pathway.
Overall response determined by balance of excitatory vs inhibitory signal strength reaching the oscillator.

Schleyer M, Saumweber T, Nahrendorf W, Fischer B, von Alpen D, Pauls D, Thum A, Gerber B. 2011. A behavior-based circuit model of how outcome expectations organize learned behavior in larval Drosophila. Learning & Memory 18:639–653. doi: 10.1101/lm.2163411.

Schleyer M, Miura D, Tanimura T, Gerber B. Learning the specific quality of taste reinforcement in larval Drosophila. Elife. 2015 Jan 27;4:e04711.

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SEVENTH FRAMEWORK PROGRAMME

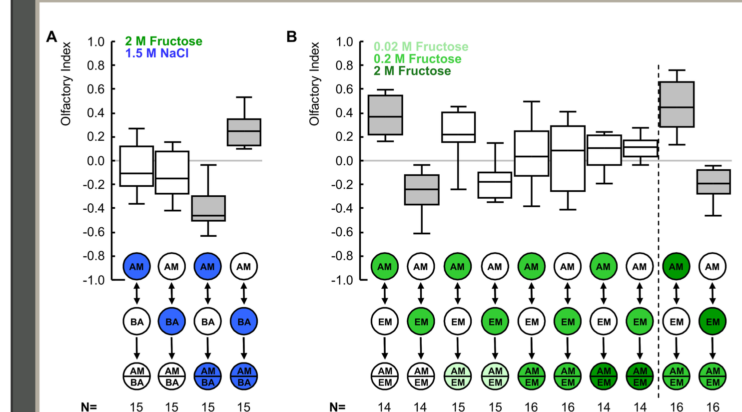
minimal

http://www.maggot.eu

Research Question

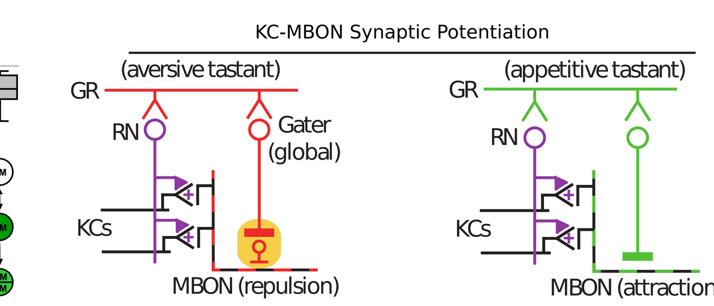
Memory is encoded via efficacy changes in KC-MBON synapses;
Learning associations induce either synaptic potentiation (P) or depressesion (D).
How can memory suppresion bypass P or D to temporarly revert to innate preferences?

Memory Suppression

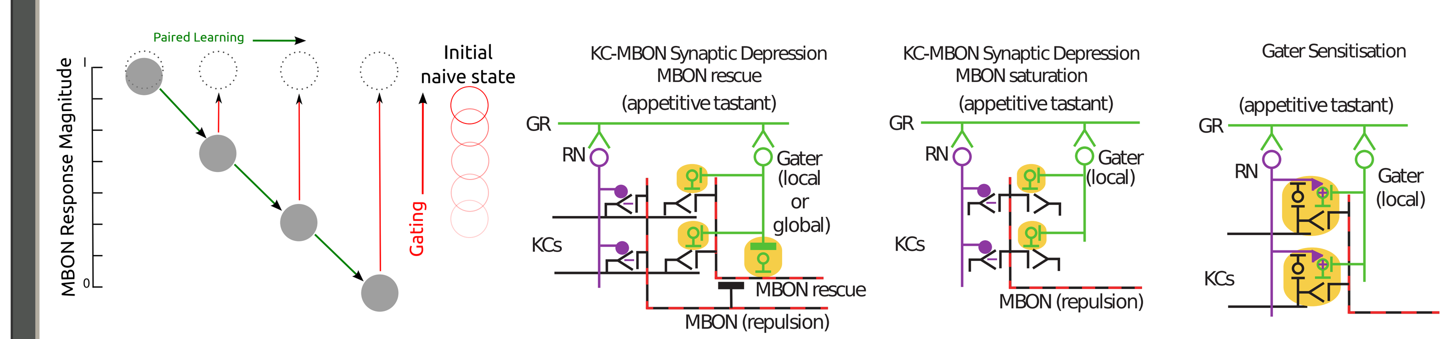


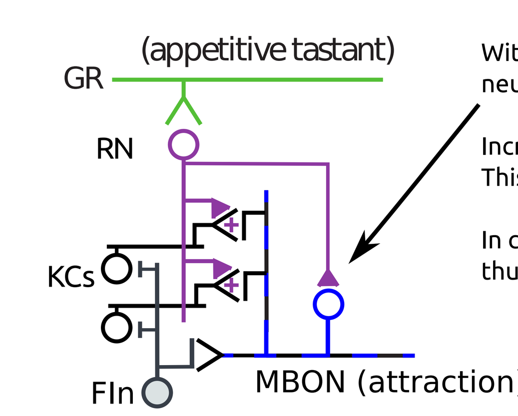
Memory expression is conditional/relative to existence of gustatory reinforcer during testing (Schleyer et al., 2011)

If learning is via *potentiation* of KC-MBON synapses then reinforcer can simply act to gate/inhibit MBON output.



If learning by *depression* then memory suppression requires the gater to re-instate the initial synaptic MBON Response. Which adds the requirement of saving this state somehow, adding to complexity :





Within the feedback circuit, this problem can be resolved by residing to neuromodulatory effects on excitability.

Increasing excitability of MBON effectively increases the gain g_1. This impairs chemotaxis, abolishing any learned approach responses.

In contrast, depressing KC-MBON synapses decreases g_1, thus improving chemotaxis for the encoded odour pattern.

Conclusions

Oscillator based chemotaxis requires input to operate around a set-point.
An integral feedback circuit can be used to maintain the set-point and transform input stimuli as pertubations around it.

The MB output can be coupled to the Oscillator to produce approach or avoidance behaviour, in an odour specific manner, via coupling MBONS to excitatory/inhibitory pathways converging to the Oscillator.
The feedback loop hypothesis predicts that gain reduction increases chemotaxis performance; thus synaptic depression at KC-MBON connections could mediate this.

Learning via synaptic depression poses a conundrum for memory suppression:
how does the gating circuit recover the initial (non-zero) synaptic levels ?
Within the feedback circuit, a neuromodulatory effect on MBONs could provide a mechanism to temporarly revert to naive state.